

Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls

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Vocally signaling a predator's presence through alarm calls creates public information regarding risk in the environment. If having this information confers an advantage, eavesdropping behavior, the use of information in signals by individuals other than the primary target, is expected to evolve. Thus, eavesdropping for information on predation risk to avoid predators may be common. We describe the first study to quantify an effect of avian alarm calling on the perceived cost of predation in a mammalian receiver/eavesdropper using the eastern tufted titmouse–eastern chipmunk dyad. We used the technique of giving-up densities to quantify changes in chipmunks' perceived risk of predation while foraging under experimental playbacks of titmouse vocalizations (seet, mobbing, and contact calls), hawk calls, and wood thrush song (control). Titmouse mobbing calls significantly increased chipmunk's perceived risk of predation. Chipmunks also appeared to divert attention (i.e., cost of multitasking) to monitoring alarm call playbacks/assessing predation risk as shown by the absence of density-dependent foraging. In contrast, when foraging during hawk calls (a direct cue of predation risk), chipmunks showed no differences in foraging relative to controls. These results support other published studies that prey respond more strongly to indirect source of information about predation risk than to direct sources. *Key words*: alarm calls, eastern tufted titmouse, eavesdropping, information, predation risk. [*Behav Ecol*]

Many groups of organisms give signals in the presence of or with the approach of a predator (Marler 1955; Searcy and Nowicki 2005). Auditory signals, referred to as predator alarm calls, are especially common among passerine birds (Marler 1955, 2005), sciurid rodents (Sherman 1985; Blumstein et al. 1997), and primates (Struthsaker 1967; Seyfarth and Cheney 1986). The function of the alarm calls and to whom the signal is intended have been widely debated and may differ among species (see reviews in Marler 2005; Searcy and Nowicki 2005). Nonetheless, alarm calls often reliably communicate the presence of a predator or increased perceived predation risk in the environment with considerable accuracy (e.g., Edelaar and Wright 2006).

Eavesdropping has been used to describe, in general terms, the use of information in signals by individuals other than the primary target (Peake 2005, p. 14). More specifically, interceptive eavesdropping (Wiley 1983) refers to signals intended for one receiver that are intercepted by another. In interceptive eavesdropping, unintended receivers or "eavesdroppers" obtain information about their environment from intentional signals given by others (as opposed to extraneous sounds; for instance, the hoof beats of fleeing antelope). Vocally signaling a predator's presence through alarm calls creates public information regarding risk in the environment (Valone and Giraldeau 1993). If having this information confers an advantage to other organisms within hearing range, eavesdropping behavior is expected to evolve (McGregor 1993;

Peake 2005). Thus, eavesdropping for information regarding risk in order to manage activity in time and space and avoid predators may be common and of significant survival value (Sullivan 1984; Dolby and Grubb 1998; Griffin et al. 2005; Langham et al. 2006). In response to an alarm call, receivers (including eavesdroppers) are expected to increase their perceived predation risk, increase vigilance, and cease risky behavior.

Passerines in the family Paridae (*Parus*, *Baeolophus*, *Poecile*) are widely recognized for their sophisticated communication, high vigilance, and aggressive nature. They detect, approach, and signal predators more readily than do coexisting satellite species within mixed species winter flocks, and these behaviors may benefit eavesdroppers through the communication of predator presence (Langham et al. 2006). Studies with parids have shown 1) changes in the vigilance of heterospecifics in association with parids in mixed species winter flocks (e.g., Sullivan 1984; Dolby and Grubb 1998), 2) greater propensity of flocking heterospecifics to move across risky habitat boundaries in the presence of titmice (Sieving et al. 2004), 3) changes in vigilance in nonflocking heterospecifics in response to playbacks of parid mobbing calls (Howell 2006), and 4) widespread heterospecific attraction to playbacks of parid mobbing calls (Langham et al. 2006).

Examples of eavesdropping between broader taxonomic gaps also exist, but it is unknown how common they might be. Squirrels associate with babbler (*Timallidae*)-led avian flocks in India and participate in alarm calling (Goodale and Kotagama 2005). Other examples of avian–mammal eavesdropping include ravens and mammalian carnivores (Berger 1999), hornbills and Diana's monkey (Rainy et al. 2004), jays and sciurids (Randler 2006), and superb starlings and dwarf mongooses (Anne and Rasa 1983). However,

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despite widely documented heterospecific avian responses to parid alarm calls, it is unknown whether coexisting small mammals with whom they may share predators eavesdrop on parids to gain information regarding predation risk in their environment.

Here we present the first study to quantify an effect of avian antipredator calls on the perceived cost of predation of a mammalian receiver/eavesdropper. Specifically, we examine eavesdropping in the eastern tufted titmouse (*Baeolophus bicolor*)–eastern chipmunk (*Tamias striatus*) dyad, 2 widely coexisting species within the temperate forest of eastern North America. We used the technique of giving-up densities (GUDs) to quantify changes in chipmunks' perceived risk of predation. We collected GUDs during vocalization playback experiments to test whether chipmunks 1) eavesdrop on titmouse vocalizations, 2) increase their perceived risk of predation in response to titmouse alarm calls, and 3) vary their perception of predation risk in response to indirect (parid alarm calls) versus direct (predator calls) sources of information.

MATERIALS AND METHODS

Study site

Experimental trials were conducted at the Institute of Ecosystem Studies (IES), Dutchess County, NY. The site contains oak-dominated deciduous forest that is home to several diurnal rodents (chipmunks, gray and red squirrels, and woodchucks) and a diverse avian community including 2 species of parids: eastern tufted titmouse (titmouse, hereafter) and the black-capped chickadee (*Poecile atricapilla*). We chose to study the titmouse–eastern chipmunk (chipmunk, hereafter) dyad because: 1) titmice have demonstrable alarm calls with predator-class and risk-based specificity (i.e., they contain information about the immediacy of the threat or type of predator; Macedonia and Evans 1993; Greene and Meagher 1998; Hetrick 2006) and 2) chipmunks are abundant diurnal rodents that are small enough to potentially share common predators with titmice.

Vocalizations and playbacks

Five different playback stimuli were broadcasted to free-living chipmunks including the call of a broad-winged hawk (*Buteo platypterus*), wood thrush song (*Hylocichla mustelina*), and 3 different titmouse vocalizations: contact calls given under low or no predation risk conditions, mobbing calls given to perched avian predators, and “seet” calls that are typically given in response to low-flying hawks or under other conditions of high perceived risk or fear/startlement (Morton 1977). Broad-winged hawks are a common raptor at IES that consume both avian and rodent prey (Goodrich et al. 1996). We obtained their characteristic high pitch whistle call from commercial sources. The wood thrush song was digitally recorded from a single individual singing at IES in May 2006 by K.A.S. The wood thrush song served as a control for chipmunk reaction to any unique sound or the speaker setup in our experiment (wood thrush are abundant at IES and frequently singing throughout the period of the study).

Playback recordings of all 3 titmouse call types were obtained from captive titmice as follows (see details in Hetrick 2006): A 2-min contact recording clip was composed of contact calls given by a flock of 3 free-flying titmice acclimated to an outdoor aviary (12 × 8 × 4 m) and behaving normally in the absence of any experimental stimuli. A 2-min mobbing clip was recorded during presentation of a live perched eastern

screech owl (*Otus asio*) to a flock of 3 titmice in the aviary. Although screech owls do not regularly prey on chipmunks, the mobbing response (i.e., harsh dee notes) that it solicits from titmice is a general response to raptors, including larger raptors, which do prey on chipmunks. The number of dee notes varies with the predator (Hetrick 2006; also see Templeton et al. 2005); however, we did not attempt to test this level of resolution by chipmunks. The recording was made during the first 2 min immediately following the unveiling of the owl in the presence of the titmice. A 2-min seet call clip was made from a composite of seet calls by 9 different captive titmice exposed to different live or model predators (snake, hawk, house cat, etc.; see Hetrick 2006). In contrast to the outdoor aviary, these recordings were made from a single titmouse housed in a 0.5 × 0.5 × 0.5-m test cage and presented with the predator 0.75 m away from the test cage.

Vocalizations were fairly evenly dispersed within individual clips, but the number of vocalizations (expressed per minute) varied: hawk call: 12, wood thrush song: 17, seet call: 20, contact call: 50, and harsh dee: 140. These differences reflect the natural pattern of vocalizing, for example, harsh dees are of short duration and given rapidly, whereas individual wood thrush songs are both longer and with a longer interval between consecutive songs. We did not attempt to control the level (i.e., number) of vocalizations at this level and doing so would be unnatural. Instead, we recorded multiple tracks of 1 of the 5 vocalizations together with periods of silence of varying time lengths onto CDs. When played with the track repeat and random track selection options, tracks were played in random order for as long as the CD player was on. Vocal tracks played 30% of the time, on average, but the pattern of vocalization with respect to random intervals of silence was determined by random shuffling of tracks. On average, this frequency of vocalizing (particularly hawk, mobbing, and seet calls) is higher than that naturally occurs. However, rapid call rates can occur over a period of 15 min or more (Schmidt KA, personal observation). Individual chipmunk foraging bouts in the food patches (see next section) take 5–20 min. Thus, a high call rate was necessary to insure that chipmunks were exposed to the vocalizations during the period of active foraging.

To broadcast the vocalizations, we used Saul Mineroff amplified speakers (model SME-AFS) attached to a CD player equipped with track repeat and random track selection functions. Titmouse vocalizations (mobbing, contact, and seet) were originally recorded under similar controlled conditions in an outdoor aviary; thus, differences in loudness during playback reflect the natural variability in intensity at which they were given during the recording process. Sound intensity during playback was measured through a sound pressure meter (flat frequency response) at 1 m: contact: 60 db; mobbing: 70 db; and seet: 80 db. The control (wood thrush song) playback was at 70 db (to match the mobbing call) and hawk playback at 80 db (to match the seet call, which is given to flying raptors). It is possible that chipmunks reacted to sound intensity rather than type, but this was inconsistent with our results (see Results); we explore this further in the Discussion.

We established 5 study sites, each located >200 m from its nearest neighbor. We used a Latin square design to randomize the 5 playback treatments among the 5 sites and over a 5-day temporal block. Under this design, each site experienced each playback only once during a 5-day block and each playback was present at a single site per day; the order of treatment presentation across time at any given site was unique. We collected foraging data using the technique of GUDs concomitant with the experimental playbacks over 3 temporal blocks, all run at the 5 sites, beginning 11 July, 18 July, and 8 August 2006, respectively, for a total of 15 days of data collection.

Giving-up densities

We used GUDs to measure changes in perceived predation risk in chipmunks in response to playbacks. Variation in GUDs from artificial food patches reflects variation in foraging costs, which include: predation, missed opportunity, and metabolic costs (Brown 1988, 1992). All else equal, increased perceived predation risk will increase the cost of predation and increase GUDs (Brown and Kotler 2004; Verdolin 2006). Thus, if chipmunks perceive higher predation risk under any of the playbacks (relative to the control), GUDs will increase. We collected GUDs from food patches consisting of a plastic tray (30 × 20 × 6 cm) containing 2 L of sifted sand and 5 g of sunflower seed fragments. Each site contained 2 feeding stations (~30 m apart), and each station contained 2 food patches side by side: a “full” patch (seeds mixed into all the sand) and a “micropatch” treatment with higher food density (seeds mixed into half the sand poured into the center of the tray while the remaining sand was filled in around the micropatch).

This dual patch design was used to detect density-dependent (or independent) harvest by chipmunks as a second means to quantify relative perceived risk. Animals foraging under elevated perceived predation risk often allocate their attention to simultaneous tasks differently than they would under safe conditions (i.e., cost of multitasking; Schmidt and Brown 1996; Kotler et al. 2004). Attention devoted to foraging tasks, such as monitoring patch instantaneous harvest rate and determining the size and location of a food patch, may be diverted to scanning or remaining alert for predators under elevated risk resulting in inefficient foragers. For example, prescient and Bayesian foragers that either possess perfect information or accumulate information, respectively, on patch quality during their foraging bout deplete resource patches in a density-dependent manner, whereas animals with little or no information forage in a density-independent manner (Iwasa et al. 1981). Although full and micropatch trays contained the same amount of food, micropatch trays had this food concentrated in only half the sand substrate within the tray resulting in higher resource density. If chipmunks elevate their perceived predation risk in response to alarm calls, we predicted that a lower proportion of stations would show density-dependent foraging under alarm playbacks.

Our experiment began after an initial prebaiting period to insure chipmunk activity and familiarity with foraging in the trays, which was confirmed by identifying chipmunk spoor. During the experiment, trays were open between 0800 and 1530 h. The playback equipment (1 speaker/CD player combination) was positioned at a height of ~1.6 m in a nearby tree approximately 20–25 m from each set of stations of trays at a site and a third speaker in between the stations. We standardized speaker placement as close as possible given the natural availability of trees to support them. At the end of each experimental day, the playback equipment was taken down, and trays were sieved to remove any uneaten food. This was taken back to the lab, cleaned of debris, and weighed to provide the GUD.

Statistical analyses

Because neither log-transformed nor untransformed GUDs were normally distributed, we followed Brown et al. (1994) in using a nonparametric analysis of variance (ANOVA) based on rank-transformed means (Conover and Iman 1981) to test for differences in GUDs among treatments, sites, and patches. All 300 GUDs were ranked from lowest to highest and averaged across treatments, patches, and stations by pooling across sites, days, and trials producing 50 ranks (5 sites × 5 treatments × 2 patch types). When compared with the results of the parametric analysis of means, the results from the nonparametric analysis were more conservative. To test for

Table 1

Results of nonparametric ANOVA based on rank-transformed means to test for differences in GUDs among treatments, sites, and patches

Effect	Degrees of freedom	Mean-square (MS)	F ratio	P
Treatment	4	2816	8.03	<0.001
Patch	1	1697	4.84	0.040
Site	4	35555	101	<0.001
Patch × treatment	4	511	1.46	>0.25
Site × treatment	16	2031	5.79	<0.001
Error	20	350		

density-dependent foraging, we compared the number of occurrences in which the high-density micropatch tray had higher GUD than its paired full patch across 2 pooled groups of treatments (alarm calls vs. all others) using a sign test. Lastly, we tested for chipmunk habituation to calls by examining GUDs across the 3 temporal blocks. We tested for decreased response using ANOVA with treatment, block, and their interaction as independent variables.

RESULTS

Chipmunks perceived their highest level of predation risk under the mobbing call and second highest levels under the seet call, with the remaining treatments (hawk, contact, and control) showing no difference (Table 1 and Figure 1). Statistically, GUDs during mobbing vocalizations were higher than all others ($P < 0.005$; Tukey HSD), whereas GUDs during seet calls were intermediate, but not statistically different from either mobbing ($P > 0.25$; Tukey HSD) or remaining treatments ($P > 0.10$; Tukey HSD). Exchanging treatment ranks into units of grams of seeds remaining showed mobbing GUDs were approximately 50% greater than control, contact, and hawk GUDs (~1.5 vs. 1.0 g) and approximately 13% greater than seet GUDs (~1.35 g). We observed a significant

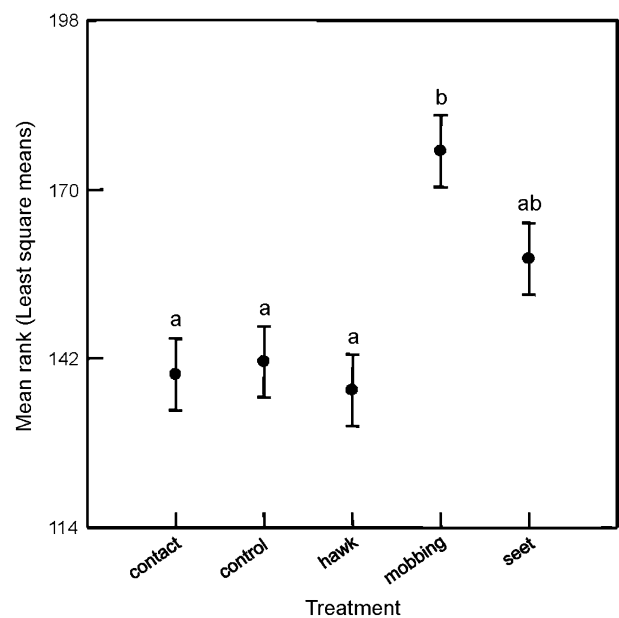


Figure 1

Mean treatment ranks (\pm standard error) based on least square means. Treatments with statistically different ($P < 0.05$) means are denoted by a unique letter.

treatment \times site interaction; GUDs during mobbing or seet were the highest at all sites except one, which was the only site where no stone wall was present near the trays (see Discussion).

Chipmunks foraged in a density-dependent manner under the treatments in which predation risk was not elevated (i.e., control, contact, and hawk; Figure 1); more food was consumed from the high-density patch in 61 of 90 (68%) trials ($P = 0.001$; sign test). In contrast, chipmunk foraging was density independent in the alarm treatments (mobbing and seet); more food was consumed from the high-density patches in only 32 of 60 (53%) trials, which is not significantly different from 50% ($P = 0.70$; sign test). There was no evidence of habituation between trials (trial: $F_{2,285} < 0.5$, $P > 0.7$; trial \times treatment: $F_{8,285} < 1.0$, $P > 0.8$ for both parametric and non-parametric ANOVAs).

DISCUSSION

Call treatments significantly affected chipmunk's perceived risk of predation as revealed through GUDs (Table 1). Compared with the control and contact playbacks, chipmunks had significantly higher GUDs during playbacks of titmouse mobbing calls and higher (but not significantly) GUDs during playbacks of titmouse seet calls. In contrast, the broad-winged hawk playback, which represents direct evidence of a predator, did not affect GUDs; nor did titmouse contact calls, which we hypothesize would indicate low risk because these calls are given when titmice are not alert for predators. Chipmunks also foraged more apprehensively under elevated risk as seen in the reduction in the frequency of density-dependent foraging under mobbing and seet calls. Thus, not only did chipmunks increase GUDs under greater perceived predation risk but also they were relatively inefficient foragers on the food they did consume, presumably through diverting attention to the increased perceived predator risk.

The lack of a response (i.e., increased GUDs) to playback of the broad-winged hawk call runs counter to our initial hypothesis. There is no ambiguity about a predator's presence when a receiver hears a predator call. In contrast, alarm calls might be unreliable if they are occasionally given when there is no real risk present (Seyfarth and Cheney 1986; Edelaar and Wright 2006), although to our knowledge this has never been quantified for the eastern tufted titmouse. We suggest that the indirect cues of risk presented by the mobbing alarm call signals a potential predatory threat, but the receiver does not obtain knowledge of the predator's 1) identity, 2) location, or 3) state (e.g., hunting or satiated). This lack of information may elicit strong apprehension by foragers, whereas in response to a predator call, the prey may obtain information on all three. Moreover, if hunting predators are usually silent, vocalizing predators may not pose an immediate risk. Interestingly, the result that receivers respond more strongly to indirect cues of risk versus direct cues of predator presence has been repeatedly demonstrated in experiments using alarm calls in birds (van der Veen 2002; Lind et al. 2005).

Site effects had a large influence on overall GUDs. More importantly, we observed a site \times treatment interaction. Whereas GUDs for mobbing and seet treatments were the highest in 4 of the 5 sites, mobbing GUDs ranked lowest (all 3 trials combined) at the site we named Crossroads. Interestingly, this was the only site that did not have a rock wall present nearby. The walls are the remnants of the boundaries between agricultural plots when land use in the area was primarily agriculture >100 years ago. Sites were originally chosen close to walls, with the one exception, because of high chipmunk activity at such sites; we presume because walls provide refuge. Although walls are generally low (i.e., 30–60 cm), irregular, and eroding, to a ground-foraging mammal, they may significantly impede

predator detection in one direction. It is possible that the combination of predator alarm calls and limited visual perception in one direction caused by the rock wall resulted in the increased cost of predation we observed. The role of habitat structure and visual impediments on perceived predation risk have been widely noted in the foraging literature (Kotler et al. 2001; Whelan and Maina 2005).

Playback volume varied by treatment in order to reflect natural variation in call volume; however, this cannot explain the significant effect of mobbing because mobbing and control playbacks had the same intensity (70 db). Neither louder hawk calls (80 db) nor softer contact calls (60 db) showed significant effects. This is not surprising if chipmunks perceive information in the call rather than responding to auditory cues based on intensity alone. It is possible that contact calls were difficult for chipmunks to hear from ~25 m away; however, the variation in signal loudness (mobbing vs. contact calls) reflects the natural conditions occurring during recording. If the lack of a response was related to sound intensity, it would suggest that the contact calls are not likely to provide chipmunks with information unless titmice are at close range.

We used a single exemplar of all playback recordings, although the actual playback sequence over time was randomized by randomizing track selection during trials. It is unlikely that chipmunks responded to some unique character of this exemplar; instead, we believe it to be a general response to the titmouse mobbing calls. The mobbing call track was recorded under presentation of a live screech owl in the aviary trials of Hetrick (2006). In 5 such trials, the number of harsh dee notes varied from 36 to 151 notes per min. Our experiment used the 140 notes per min track and thus represents the high end of the range recorded by Hetrick (2006). A key component of the mobbing call that increases with risk is the number of "harsh dee" notes comprising the second part of the "chickadee" call complex (Dixon 1955; Templeton et al. 2005; Hetrick 2006); thus, a lower number of dee notes may moderate the responses we detected; however, we did not attempt to test this level of resolution by chipmunks. These recordings have also been used to document heterospecific responses by black-capped chickadees and northern cardinals (*Cardinalis cardinalis*; Howell 2006). Finally, other work within our laboratory demonstrated that other cotton rats (*Sigmodon hispidus*) showed consistent responses (increases in GUDs) to 2 different blue jay (*Cyanocitta cristata*) scolding recordings in Texas (Felts 2007) and gray squirrels showed consistent responses to 3 different jay recordings at our site in New York (Schmidt and Ostfeld 2008; for similar results, also see Randler 2006).

One last caveat is that chipmunks may have responded to the actual presence of titmice responding themselves to the playbacks. When humans mimic the harsh dee notes of the mobbing call by "pishing," it can attract the presence of multiple titmice (Langham et al. 2006; Schmidt KA, personal observation). After setup, we vacated the area so as to not disrupt or influence chipmunk foraging, and thus, we could not make observations to rule out titmouse attraction to the playbacks. We strongly suspect that chipmunks were not responding to titmice attracted to the playbacks, largely because we have observed that titmice quickly disperse (~5 min or less) after cessation of mobbing calls, human pishing, or titmouse playbacks. Because chipmunk arrivals at the foraging patches were typically delayed $\gg 5$ min after beginning the playbacks, we suspect that any attracted titmice would have dispersed before foraging began. Nonetheless, we suspect chipmunks would respond, additively or multiplicatively, to multiple cues when present, such as mobbing calls and the physical presence of titmice.

Although previous studies have demonstrated cross-species transfer of information between birds and mammals, this is the

first study to quantify an effect of avian antipredator calls on the perceived cost of predation of a mammalian receiver/eavesdropper. Randler (2006) demonstrated that red squirrels (*Sciurus vulgaris*) respond to playbacks of Eurasian jays (*Garrulus glandarius*) by increasing the frequency of vigilance behaviors (e.g., head turning) and increasing the latency to resume foraging after jay playback. Yellow-casqued hornbill (*Ceratogymna elata*) reactions to the unique leopard and eagle alarm calls of Diana's monkey (*Cercopithecus diana*) are statistically identical to their reaction to actual leopard call and eagle scream (Rainey et al. 2004). Thus, not only does the information transfer occur but also does the specific content concerning predator types. This body of work clearly demonstrates that cross-taxa information transfer readily occurs between mammals and birds in either direction. It remains uncertain whether this behavior has significant survival implications or other long-term benefits.

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